

PSYCHE.

IMAGINAL DISCS IN INSECTS.

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Among insects which have a complete metamorphosis the organization of the larva is in general similar to that of the adult or imago, but the larva always lacks certain organs which the imago possesses. The larval beetle or butterfly lacks wings, the larval bee has neither wings nor legs which is also true of the larval gnat, while the larval fly has neither legs, wings nor head; and in each case the imago possesses these organs. As we ascend the scale of development from the less highly to the more highly specialized insects having complete metamorphosis, we find a constantly increasing sum of differences between the larval and the imaginal forms, and a correspondingly increasing number of organs which are possessed by the imago and not by the larva. This drawing apart is due, on the one hand, to the higher specialization of the imago and its consequent further departure from the ancestral stage of its ontogeny represented or suggested by the larva, but also largely to the retrogressive development of the larva itself. In the highest insects, where the imago is a highly specialized animal capable of living only in a certain restricted environment, the larva is perhaps as

highly specialized as is the imago: its environment is as sharply restricted and its structure departs as far from the phyletic type or stage it represents as is the case with the imago.

In the coleoptera, to consider first one of the less highly specialized groups of holometabolic insects, the environments of the larva and of the imago are usually quite similar, or perhaps they are exactly the same; the organs of the two forms are correspondingly similar, and the transformations which must be accomplished on the body of the larva to produce the imago are but slight. The imago differs from the larva principally in that it has acquired wings, elytra, compound eyes, and external reproductive organs, but all the larval organs with the exception of the midgut become imaginal ones without great change. The midgut in all holometabolic insects undergoes a complete transformation during the metamorphosis.*

In the lepidoptera, to come to a somewhat more highly specialized group, the larval and imaginal environments are apparently widely different

* Kowalevsky, A. Beiträge zur Kenntnis der nachembryonalen Entwicklung der Musciden. Zeit. f. wiss. Zool. 45: 3, 1887, p. 505.

from each other. But, after all, both larva and imago live on vegetable food, and more than this, in the higher members of the group at least, on very nearly the same kind of vegetable food, the leaves and flowers of phanerogamous plants. The larva eats and lives among the green leaves, while the imago finds its nourishment in the flowers which are modified leaves. So that we shall not be surprised if we find that the transformations which result in the production of the butterfly from the caterpillar are not as great as the apparently great difference between the two forms might suggest. As is the case with the coleoptera, the imago acquires wings, compound eyes, and external reproductive organs, and all the larval organs with the exception of the midgut pass directly into the imaginal organs, although some of them are highly modified in the process; but there is no complete making over, no general histolysis.

In the hymenoptera the larva and imago live in general on the same kind of food. But the conditions of colonial and family life which prevail among the higher members of the order have resulted in a marked retrogressive development on the part of the larva, so that it is very different structurally, from the imago. Not having to find its own food, to protect itself, or to escape from enemies, it has lost its extremities. In the nematoceran diptera other conditions have produced similar results, and we also find apodous larvae. The transformations, now, which the pupae of these

insects must undergo to become imagines are much greater than is the case in the coleoptera or lepidoptera. Not only must wings be acquired during the metamorphosis but legs as well, and the larval organs require a much greater modification before they can serve as imaginal organs. But yet no complete making over, no general histolysis* takes place.

When we come to the brachyceran diptera, the most highly specialized insects in my opinion, we find the greatest structural differences between the larva and the imago to be met among insects. The environment of the larva is as a rule totally different from that of the imago, and the larval structure correspondingly different from the imaginal. The larva, too, has undergone an extensive retrogressive development. In the case of the nematocera, as I have just said, the larva is without legs, but in the brachycera the retrogression has gone much further and the larva has neither legs nor head. There are also great internal differences. In the metamorphosis, consequently, a very different animal must come out of the puparium than went into it. The imago must acquire not only external reproductive organs, compound eyes, wings, legs, and a head, none of which the larva possessed, but also internal organs very different from those of the larva. A complete making over accompanied by general histolysis is the result.

* Ganin, M. The post embryonic development of insects. (Russian) Warsaw 1876. Reviewed in Zeit. f. Wiss. Zool. 28Bd. 1877: p. 380.

A dissection of an old larva or a young pupa of either of the insect orders above mentioned would show that these new organs which the insect is to acquire during its metamorphosis are really already present, not as fully formed organs, however, but in the form of rudiments oranlagen. In the body cavity of the caterpillar, for instance, buried beneath the dorsal meso- and metathoracic integument are two pairs of small disc-like islands of cells. These remain unfunctional and inactive during the caterpillar's lifetime although growing constantly, but during its metamorphosis they develop into the two pairs of wings of the butterfly.* Similar cell-islands are present in the larval coleopteron.† The larval hymenopteron also possesses them‡; while beneath its ventral thoracic integument are three other pairs of cell-islands whose fate it is to furnish the imaginal legs. In the nematocera, also, ventral and dorsal pairs of cell-islands are present in the larva, as the observations of Weismann on *Corethra* ‡ first showed. This classic investigation demonstrated the presence of three dorsal pairs of cell-islands as well as three ventral pairs. They are situated in the body cavity of the larva just beneath the integument, a dorsal and a ventral pair in the prothorax, destined to form the pupal spiracles and the

imaginal prothoracic legs, respectively; a dorsal and a ventral pair in the mesothorax, destined to form the wings and the mesothoracic legs; and a dorsal and a ventral pair in the metathorax, destined to form the balancers and the metathoracic legs.

In the brachycera Weismann § was again the first to prove the existence of these cell-islands. It was in 1864 that he published in his account of the post-embryonic development of the muscids the first correct and extended observations on these peculiar cell-islands in any insect. He called them *imaginal discs*. He showed that in *Musca* six pairs are present in the larval thorax, not near the surface as in *Corethra*, but in the center of the larva, and that their fate is exactly the same as in *Corethra*. In addition to these thoracic imaginal discs he described two large cephalic discs situated in the forward portion of the thorax and connected with the larval pharynx, the fate of which is to form the imaginal head. Weismann also showed ¶ that but a small portion of the larval body passes directly into the imaginal body, but that most of it undergoes disintegration so that the different tissues entirely lose their identity, after which the imaginal body is built up from the imaginal discs. To this process, the entire significance of which was not, however, understood until later, he gave the name *histolysis*.

*Swammerdam. Bibel der Natur. Leipzig 1752, p. 3. Pan-critins. Beitr. z. Kennt. d. Flügelentw. b. d. Insecten. Königsberg, 1884.

† Ganin. l. c. p. 387.

‡ Weismann. Die Metamorphose von *Corethra plumicornis*. Zeit. f. wiss. Zool. 16 Bd. 1866. p. 45.

§ Weismann, A. Die nachembryonale Entwickl. d. Musciden nach Beob. an *Musca vom.* u. *Sarcophaga carnaria*. Zeit. f. wiss. Zool. 14 Bd. Heft 3. 1864. p. 221.

¶ l. c. p. 322 and 326.

These observations of Weismann opened a new field of investigation in the development of insects. This has been entered by several eminent investigators of whom Ganin, Künckel d'Herculais, Viallanes, Kowalevsky, and Van Rees have been the most successful. Ganin * in 1876 demonstrated the presence of many other imaginal discs than those which Weismann described. Weismann supposed that the hypodermis of the larval abdomen went directly with some modifications to form that of the imago. Ganin showed, now, that in the hypodermis of each of the eight abdominal segments are four cell-islands, two dorsal and two ventral, which resemble in every respect the tissue of the imaginal discs; that they are in fact imaginal discs and are destined to form the starting points for the growth of the imaginal abdominal hypodermis. Ganin also discovered similar discs in the epithelium of the midgut whose fate it is to form, in the same way, the imaginal midgut, and also the important fact that each imaginal disc in the larva is made up of two kinds of embryonic tissue, ectoderm and mesoderm or mesenchym. In 1875 Künckel d'Herculais † found in the last abdominal segment two pairs of imaginal discs of the external genital organs. In 1883 Metschnikoff ‡

published the first of his epoch-making observations on the destruction of tissues in certain invertebrates by leucocytes or as he called them phagocytes. He discussed Ganin's paper and especially his statement that during the histolysis of the pupal muscid the larval organs are destroyed by amoeboid mesoderm cells. These cells he suggests are none other than phagocytes. In 1884 Van Rees § and in 1885 Kowalevsky || proved the correctness of this position; they showed that the process of histolysis is the tearing down and digestion of the functional larval tissues by phagocytes and the building up of imaginal tissues from imaginal discs.

In 1888 Van Rees ¶ published his extensive paper on the post-embryonic development of muscids, and completed our knowledge of this phenomenon. He showed that when the muscid larva has entered upon the pupal stage, histolysis is inaugurated by the destruction of the larval muscles, they becoming unfunctional directly after pupation and a natural prey to the phagocytes. Soon the thoracic hypodermis and the inner organs are attacked, and at the same time the imaginal discs begin to grow and widen out to supply the place of the tissues which are being destroyed. The continuity of the hypodermis and

* l. c. p. 386.

† Künckel d'Herculais. Recherches sur l'organisation et le développement des Volucelles. Paris, 1875, p. 149.

‡ Metschnikoff. Untersuchung über intracelluläre Verdauung bei Wirbelosentieren. Arb. a. d. Zool. Inst. z. Wien. 5 Bd. 1883, p. 147.

§ Van Rees. Over intra-cellulaire spijsverteering en over de beteekenis der witte bloedlichampjes. Maandblad voor Naturwetenschappen. Jaarg. 11, 1884.

|| Kowalevsky. Beiträge z. nachembryonale Entwicklung d. Musciden. Zool. Anz. 8 Bd. 1885, p. 98.

¶ Van Rees. Beiträge z. Kenntniss d. inneren Metamorphose v. Musca vomitoria. Zool. Jahrb. Abth. t. Anat. u. Ontog. 3. Bd. 1888, p. 1.

of most of the internal organs is thus not at any time broken. As these processes go on, the two large head imaginal discs, which form two irregularly shaped sacks extending as diverticula from the dorsal wall of the pharynx back to the brain, begin to pass forward dragging the brain with them. Their anterior ends bend and pass ventrad embracing the pharynx between them. At the same time their communications with the pharynx enlarge and their lumena fuse more completely with the pharyngeal lumen. These communications now continue to enlarge; they fuse into one single median opening which, ever increasing in size, travels from the anterior end of the pharynx posteriorly, obliterating the dorsal pharyngeal wall in its course. Finally the lumena of the discs and that of the pharynx become completely merged and form together a single continuous space, and the walls of the discs and of the pharynx form a single continuous vesicle. This is the head-vesicle of Weismann* and Van Rees† which is destined to become the imaginal head. On its anterior ventral surface epithelial thickenings appear which are destined to form the imaginal antennae and mouth parts, while at its posterior end are thickenings which are to become the compound eyes and which are still in contact with the brain. The head-vesicle remains buried within the pupal thorax until near the end of the pupal

period when it evaginates and forms the imaginal head. This evagination has been observed by Weismann‡ to be the consequence of the pressure of blood which at the right moment rushes from the abdomen into the thorax and pushes the head-vesicle forward.

The metamorphosis of the thorax goes on simultaneously with the formation of the head-vesicle. In proportion as the larval hypodermis disappears under the attacks of the phagocytes, as I have already mentioned, the edges of the imaginal discs grow and take its place, forming the imaginal hypodermis. As we have seen, there are six pairs of these discs, three dorsal and three ventral, and they are in the center of the larva. Each disc is, however, connected with that portion of the hypodermis of the segment to which it genetically belongs and where it is destined to appear as an extremity, by a very fine, hollow chord. This chord, now, begins to shorten and its lumen to enlarge. The disc is thus brought nearer the surface and, as it advances, it increases in size. The lumen of the chord then opens through the hypodermis to the outside, and finally becomes so wide and the chord itself so short that the disc is brought through the hypodermis to the outside. The hollow chord has of course been obliterated by this process and the edges of the proximal end of the disc brought into direct connection with the hypodermis. The disc has by this time assumed its

*l. c. p. 258.

†l. c. p. 44.

‡l. c. p. 259.

position as an extremity. It is an appendage of the body wall; it has become irregularly cylindrical in shape and possesses a number of constrictions and folds, which in the case of the ventral discs are equivalent to the joints of the future leg. The proximal edges of the discs, those in contact with the larval hypodermis, grow and extend themselves and take the place of larval hypodermis in proportion as this is destroyed by phagocytes.

The metamorphosis of the abdomen is retarded and does not begin until that of the head and thorax is well advanced. Then in each abdominal segment the two ventral and four dorsal discs (Van Rees found two additional dorsal discs in each segment) begin to grow and take the place of the disappearing larval hypodermis.

Kowalevsky * discovered that the discs of the last segment do not take part in the formation of hypodermis, but of the endgut with the rectal glands, and that they are situated in the vicinity of the larval anus. The metamorphosis of the larval internal organs was correctly reported first by Kowalevsky † in the year preceding the publication of Van Rees' paper. All of these organs are destroyed by phagocytes except the central nervous system, the heart, the reproductive organs, and three pairs of thoracic muscles. These with the exception of the reproductive organs remain

active, functional organs during the pupal period and are not attacked by phagocytes, but pass directly into the imago without great change and become imaginal organs. The organs destroyed are reconstructed from imaginal discs in a way similar to that already described.

The only paper dealing with imaginal discs which has appeared since Van Rees' is one of my own published in 1893.‡ It contains a description of the larva of *Melophagus ovinus*, a pupiparous dipter.

The pupipars are cyclorrhaphic brachycera and very closely allied to the muscids, so that we may expect to find the same imaginal discs in their larvae as in the muscids. And we do, in fact, find in general similar conditions, but there are several interesting differences. The larva is apodous and acephalous like the muscidian, but in many respects it is much less highly specialized: it seems, in fact, as if it might represent the ancestral stage in dipteran phylogeny at which the muscids are beginning to draw away from their relatives, to occupy a position between *Corethra* and *Musca*. In the position of the thoracic discs, for instance, it closely resembles *Corethra*. We find these discs just beneath the integument in two very regular rows and not in the center of the larva as in *Musca*. The accompanying wood cut represents dorsal and ventral frontal

* Kowalevsky. Beiträge z. Kenntniss d. nachembryonalen Entwicklung d. Musciden. I Theil. Zeit. f. Wiss. Zool. 45 Bd. 1887, p. 557.

† l. c. p. 542

‡ Pratt. Beiträge z. Kenntnis d. Pupiparen. Die Larve von *Melophagus ovinus*. Archiv f. Naturgeschichte. Bd. 59. 1893, p. 151.

sections through the anterior end of an old larva showing the position of the thoracic discs. The dorsal prothoracic

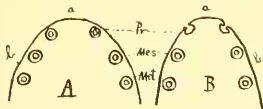


Fig. 1. *A*, ventral frontal section; *B*, dorsal frontal section; *a*, anterior-pole; *Pr*, *Mes* and *Met*, pro-, meso-, and metathoracic imaginal discs; *b*, body wall.

pair arise during the larval period and are not embryonic organs as are all the others (Van Rees noticed the same fact about the corresponding muscidian discs). They are invaginations of the larval hypodermis and have external openings which do not close, and their inner surface is lined with a delicate cuticula which is a continuation of the external cuticula of the larva. These discs are rudimentary organs and do not develop into any pupal or imaginal organs. In structure the meso- and metathoracic discs stand exactly midway between the same discs in *Corethra* and in *Musca*. In *Corethra** all the thoracic discs are of larval origin, aris-

ing as they do after the last larval moult, and each one is a double fold of the hypodermis, of which it remains a part as Fig. 2 shows. In *Melophagus*, on the other hand, each of these discs arises in the embryo, as is also the case in *Musca*; it is also a double fold of the hypodermis but becomes constricted off from it as is shown in Fig. 3. Van Rees'† has called that portion of the invaginated hypodermis which encloses the disc proper, the parapodial membrane (*P*, Figs. 3 and 4), and the space it encloses, the parapodial space. In *Musca*‡, now, the disc not only becomes constricted off from the hypodermis but suffers removal to the center of the larva as is shown diagrammatically in Fig. 4, and the parapodial membrane lengthens to form the hollow chord which connects it

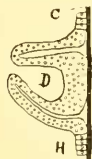


Fig. 2. *D*, imaginal disc in *Corethra*; *H*, hypodermis; *C*, cuticula.

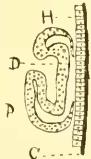


Fig. 3. *D*, imaginal disc in *Melophagus*; *H*, hypodermis; *C*, cuticula; *P*, parapodial membrane.

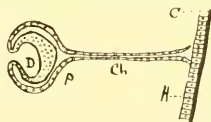


Fig. 4. *D*, imaginal disc in *Musca*; *H*, hypodermis; *C*, cuticula; *P*, parapodial membrane; *Ch*, chord.

with its old position at the hypodermis. The fate of the thoracic discs in *Melophagus* is exactly the same as in *Corethra* or in *Musca*.

In the cephalic discs, now, we find the conditions similar to those in *Musca*, but even more complicated. Instead of a single pair of head-discs we find two pairs, one dorsal and one ventral. The dorsal pair corresponds to the muscidian

* Weismann, *Corethra*. l. c. p. 78.

† l. c. p. 24.

‡ Van Rees. l. c. p. 23.

head-discs in every respect; they are destined to form the dorsal and lateral portions of the imaginal head together with the compound eyes. The ventral head-discs have no counterpart in *Musca*. In the embryo, as we shall see in a moment, they appear as a single median thickening, but in the young larva they have become paired diverticula of the ventral pharyngeal wall; and at the bottom of each diverticulum there arises a projection. These diverticula soon fuse in the median line and the wall between them gradually disappears. In the old larva, consequently, the ventral discs appear as a single ventral diverticulum of the pharynx at the bottom of which a pair of long projections extend toward the wide opening. The fate of these discs is to form the ventral portion of the head, the paired projections forming the anlage of the proboscis.

The formation of the head-vesicle proceeds in a way similar to that in *Musca*. The ventral disc fuses early at its lateral edges with the dorsal pair. The communications between both ventral and dorsal discs and the pharynx rapidly widen (in the old larva they have already become very large), and soon the discs and pharynx form together a single vesicle, which is the head-vesicle.

The imaginal discs of the abdomen in *Melophagus* are exactly the same as the corresponding ones in *Musca*.

I shall now speak of the origin and early development of imaginal discs. But little has been published on this subject and nothing, so far as I know, on the origin of muscidian discs.

Weismann* showed in 1866 that in *Corethra*, that is, in the nematocera, the thoracic discs arise as ectodermic infoldings after the last larval moult, and just before pupation (Fig. 2). This is rather surprising, as we should expect these discs, as they represent extremities, to appear in an early embryonic period when the extremities usually arise in insects. In *Musca*, Weismann† did in fact find that the imaginal discs arise in the embryo, but their genesis was not observed by him, and, as he found them invariably attached to a trachea or a nerve, he made the mistake of supposing that they take their origin in the epithelial coverings of these organs. This method of growth was, however, early discredited by Künckel d'Hercule‡ who, in 1875, found the chord connecting the thoracic discs with the hypodermis, and rightly concluded that they have an ectodermic origin. Balfour§ also, in his text book, declared that the thoracic and cephalic discs must be derivatives of the ectoderm in *Musca* as they had been proved to be in *Corethra*. Dewitz|| in 1878 confirmed d'Hercule's observation of the chord connecting the disc with the hypodermis, and Van Rees some years later in his paper already quoted¶ showed that this chord is

*Weismann. Die Metamorphose v. *Corethra* etc. p. 78.

†Weismann. Die nachembry. Entw. v. d. Musciden, etc., p. 223.

‡l. c. p. 146.

§Balfour. Comparative Embryology, vol. 1, p. 423.

||Dewitz. Beiträge z. Kenntnis d. postembry. Gliedmassen b. d. Insecten. Zeit. f. wiss. Zool. Bd. 30, Sup. p. 95.

¶l. c. p. 25

hollow, that its lumen is a continuation of the parapodial space, as shown in Fig. 4, and that both lumen and parapodial cavity are lined by a fine cuticula. He asserts that this discovery is anatomical proof that the chord, the parapodial membrane, and the disc itself are all parts of a single invagination of the embryonic ectoderm. Graber,* however, in 1889, supported by certain observations on *Calliphora*, a muscid, asserts that the beginnings of both the thoracic and cephalic imaginal discs are not ectodermic invaginations, but ectodermic thickenings towards the inside, followed by delaminations.

There exists in fact at the present time no embryological evidence on the origin and first stages of development of the thoracic and cephalic imaginal discs in the brachyceran diptera, although all the later writers except Graber, supported by the fact of their undoubted ectodermic origin in the larva of *Corethra*, and also by the anatomical evidence adduced by Van Rees, are of the opinion that they arise as invaginations of the embryonic ectoderm.

I have been for some time studying the embryonic development of *Melophagus ovinus*, and, although the study is not yet completed, I am able to give a detailed account of the origin and early history of the imaginal discs in this insect. *Melophagus* is a cyclorrhaphic brachyceran. Leuckart† early showed

the striking similarity of its larval and pupal forms, and of the pupipars in general, to those of the muscids; in an earlier portion of this paper, I have emphasized the same fact: Müggenburg‡ has described the mouthparts of almost all the pupipars and homologised them with the parts of the fly's proboscis; Brauer§ considers the pupipars degenerate flies. The relationship between the pupipars and the muscids is undoubtedly a very close one, and observations on the former must be conclusive in determining the method of origin of imaginal discs in the latter, as well as in all the higher diptera.

In *Melophagus* the cephalic and thoracic imaginal discs first appear as local thickenings followed by invagination of the embryonic ectoderm. The cephalic discs make their appearance first, and very early in the ontogeny of the insect. The ventral plate, as in other diptera, is not confined to the ventral side of the embryo, but it encircles the anterior end and covers the anterior third of the dorsal side, as is shown in Fig. 5. The stomatodeum appears as an ectodermic depression on the dorsal side at some distance from the anterior end (S, Fig. 5), the proctodeum as a corresponding depression on the dorsal side, slightly distant from the posterior end (P, Fig. 5). These are not, however, the permanent positions of

* Graber. Vergl. Stud. über d. Embry. d. Insecten. Denks. Acad. Wiss. z. Wien. Bd. 56, p. 306.

† Leuckart. Die Fortpflanzung u. Entwick. d. Pupiparen. 1858

‡ Müggenburg. Der Rüssel d. Diptera pupipara. Archiv f. Naturgeschichte. Jahrg. 58, 1892, p. 287.

§ Brauer. Systemat.-zool. Studien. 91 Bd. d. Sitzungsbr. d. Kais. Acad. d. Wiss. 1st Abt 1885, p. 405.

these organs. They gradually migrate towards the two poles of the egg, and finally attain positions slightly ventral

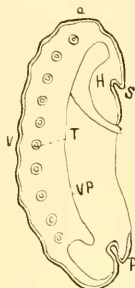


Fig. 5. Embryo *Melophagus*, side view; *a*, anterior end; *V*, ventral side; *S*, stomatodeum; *P*, proctoderm; *VP*, ventral plate; *T*, tracheal invaginations; *H*, head-fold.

to the anterior and posterior poles respectively. Long before the stomatodeum has attained its definitive position, however, there appear before and behind it crescentic, ectodermal thickenings which partly encircle it as shown in Fig. 6. These are the begin-



Fig. 6. Anterior end of embryo, dorsal view; *H*, head-fold; *S*, stomatodeum; *VD*, ventral disc; *DD*, dorsal discs.

nings of the cephalic imaginal discs, which, it will be seen, appear very early in the ontogeny of the insect,

while, in fact, the intestinal tract, the tracheal, and nervous systems are in their first anlagen. The crescentic thickenings, now, are three in number, a pair just behind (*DD*, Fig. 6) and a single median one just before (*VD*, Fig. 6) the stomatodeum. The latter thickening is destined to form the ventral cephalic disc; the fate of the pair, on the other hand, is to form the dorsal discs, those homologous with the cephalic discs of *Musca*. At the posterior side of each of the latter thickenings, now, an invagination begins to appear which finally becomes a deep pocket. Each pocket early shows an intimate connection with a supra-oesophageal ganglion, the latter abutting the posterior side of the pocket, but having no structural union with it. During the formation of these pockets, however, the stomatodeum, together with the dorsal and ventral discs, has been continuing its migration towards the anterior end of the embryo, and the formation of the intestine and closure of the back of the embryo have been going rapidly forward. Finally, when the mouth has arrived at its definitive position at the anterior pole of the embryo, the dorsal pockets have come to occupy a position on the dorsal side of the embryo just above it, and the back is entirely closed.

The openings of the pockets have by this time moved to the mid-dorsal line and merged into a single median opening. In Fig. 7, *DD* represents this common opening. The proximal or upper portions of the pockets have also fused, but their distal ends are still free

from each other and each still abuts a supra-oesophageal ganglion. As to the median ectodermic thickening in Fig. 6 (VD) which is destined to form

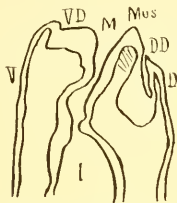


Fig. 7. Sagittal section of anterior end of embryo just before involution of head; *M*, mouth; *I*, intestine; *V**D*, ventral disc; *DD*, dorsal discs; *Mus.*, muscle projection; *V*, ventral side; *D*, dorsal side.

the ventral cephalic disc, it migrates forward with the stomatodeum, suffering at the same time a slight invagination, and finally takes a position immediately below the mouth (*VD*, Fig. 7). The relation of the other organs of the anterior portion of the embryo to the discs, is well shown in Fig. 7. Just dorsad of the mouth and between it and the median portion of the dorsal discs is seen a muscular projection (*Mus.*) whose later history will be found to be interesting.

A very important change now takes place in the development of the animal, namely, the involution of the embryonic head. An ectodermic fold starts just posteriad of the discs, both dorsal and ventral, and grows rapidly forward towards and over the mouth. The mouth, with the ventral disc just ventrad of it and the muscular projection and dorsal discs just dorsad of it, is rolled in

by this process. A new mouth is formed (*M*, Fig. 8) and just back of it is a new portion of the intestinal tract (*P*, Fig. 8). This is the so-called pharynx of Weismann and Van Rees, described by them in the larva of *Musca*. Just back of the pharynx is the oesophagus and the old mouth, dorsad of which is the muscular projection (*Mus.* Fig.

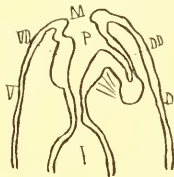


Fig. 8. Sagittal section of embryo just after involution of head; *M*, mouth; *P*, pharynx; *DD*, dorsal discs; *V**D*, ventral disc; *I*, intestine; *Mus.*, muscle projection; *V*, ventral side; *D*, dorsal side.

8). This projection becomes in the larva the most active organ in the animal. It is a sucking tongue and by its regular pulse-like contractions causes a flow of the milk-like secretion, which is present in the uterus and forms the food of the larva, into the mouth.* Connected with the dorsal wall of the pharynx is the fused median portion of the dorsal discs (*DD*, Fig. 8) which in Fig. 7 opened to the outside of the embryo. The distal portions of the discs represent diverticula which extend back to the supra-oesophageal ganglia. On the ventral side of the pharynx is the ventral disc (*VD*, Fig. 8) which shows a slight invagination and which is destined to undergo considerable changes

* Pratt. l. c. p. 170.

before it reaches its final form.* The forward end of the animal does not change materially, now, from the condition we find represented in Fig. 8 during the remainder of the embryonic and the entire larval period. Early in the pupal period, however, the dorsal and ventral discs unite to form the head vesicle, as explained in a previous portion of this paper, which becomes the imaginal head.

So much for the origin and embryonic history of the cephalic imaginal discs. The thoracic discs (with the exception of the dorsal prothoracic which arise in the larva) do not make their appearance until the time of the involution of the head. This is late in the embryonic life and at a period when its organization and the formation of the head discs are completed. The thoracic discs arise, like the cephalic, as ectodermic thickenings. A dorso-ventral section to one side of the median line of the same embryo of which Fig. 8 represents a sagittal section, is shown in Fig. 9. The

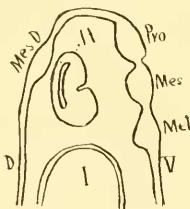


Fig. 9. Dorso-ventral section of anterior end of embryo; *Pro*, *Mes*, and *Met*, ventral pro-, meso-, and metathoracic discs; *Mes. D*, dorsal mesothoracic disc; *H*, head-disc; *I*, intestine; *D*, dorsal side; *V*, ventral side.

three ventral ectodermal thickenings are the beginnings of the ventral pro-meso- and metathoracic imaginal discs on one side of the embryo. The dorsal thickening is the beginning of the dorsal mesothoracic disc. The dorsal metathoracic disc does not appear in this section. All these discs begin very soon to invaginate, the ventral prothoracic beginning first, then the mesothoracic, and finally the metathoracic taking its turn. The invagination begins in each disc at its posterior border as is shown in the ventral metathoracic disc in Fig. 10; then the anterior border sinks in as is shown in the mesothoracic disc in Fig. 10; finally the entire disc sinks beneath the surface as is shown in the prothoracic disc in Fig. 10; then the ecto-



Fig. 10. *Pro*, *Mes*, and *Met*, ventral pro-, meso-, and metathoracic discs, showing beginning of invagination.



Fig. 11. Disc with invagination completed.

derm closes over it as is shown in Fig. 11, at which stage it is comparable to the thoracic discs in *Corethra* as represented in Fig. 2. The disc now becomes separated from the ectoderm, the thickened middle portion sinks in and forms the disc

* Pratt. l. c. p. 188.

proper, the real anlage of the extremity, while the portion at the side becomes the parapodial membrane, and the disc is formed as we find it throughout the larval period (Fig. 3).

As to the discs of the internal organs and of the abdominal hypodermis, I have not observed them in the embryo and think it is probable they appear first in the larva.

Before closing I wish to dwell for a moment on one or two theoretical questions which naturally present themselves. In the first place, why is it that in the brachyceran dipters the phagocytes, that is the blood corpuscles, during the metamorphosis do not attack all the larval tissues indiscriminately instead of being selective in their operations. We find that in the histolysis certain organs only, such as the larval hypodermis, intestine, muscles, etc., are attacked and destroyed while others, such as the imaginal discs, the heart, central nervous system, reproductive glands, and even some of the muscles are left intact. Kowalevsky* seeks to answer this question. He says the reason is the same as that which accounts for the fact, first observed by Metschnikoff,† that certain *virulent* bacteria, as the form which is the cause of Anthrax, are not attacked by leucocytes, while the same form in Pasteur's vaccine for Anthrax, which has been weakened and robbed to a certain extent of its virulent power, is attacked and consumed. With

the beginning of the pupal stage in Musca the larval tissues, being no longer active, functional tissues, become weak and degenerate and are attacked and destroyed by the amoeboid blood corpuscles of the pupa, as are the non-virulent bacteria of the vaccine by the leucocytes. The imaginal discs, on the other hand, which are a fresh, young tissue, whose cells are rapidly proliferating, are immune, as are also the virulent bacteria. Kowalevsky also says that perhaps the tissue of the imaginal discs also secretes some substance which renders it secure against the attacks of phagocytes as do the virulent Bacteria. Van Rees‡ says that the phagocytes do, as a matter of fact, attack all the larval organs indiscriminately, but that the active metabolism of the cells of the imaginal discs preserves them from these attacks. He thinks Kowalevsky is probably right in supposing that the discs render themselves immune by some poisonous secretion.

It seems to me that the supposition of a protecting secretion is hardly necessary to account for the phenomenon, and it certainly would not account for the preservation of those functional larval tissues which are not destroyed. As soon as the larval life is over, in those organs and tissues which then become functionless and inactive, a healthy metabolism would cease, and they would begin to exhibit signs of weakness and degeneracy. In this condition they would be an easy prey to phagocytes or disintegrating influences of any sort.

* I. c. p. 555.

† Metschnikoff. Archiv f. pathol. Anat. Bd. 97, p. 512.

‡ I. c. p. 120.

Weak or functionless organs in any animal are peculiarly susceptible to disease. Healthy organs may be exposed to the same influences without danger. In the same way the imaginal discs, in which there is an exceedingly active metabolism, and *all the larval organs which remain functional during the metamorphosis* or during a greater part of it are immune from the attacks of the phagocytes. The heart in the muscids continues to beat, as Künckel d'Herculis has observed, during the entire period of the metamorphosis with the exception of a day or two in the latter half of it. The nervous system must continue functional during the entire time. The three pairs of thoracic muscles which pass intact from the larva to the imago are probably employed in respiration during the metamorphosis. The reproductive glands are, like the imaginal discs, rapidly growing organs. It would be interesting to know exactly to what extent the blood corpuscles in the other orders of insects besides the brachyceran dipters become phagocytes during the metamorphosis, and why histolysis is so much more extensive here than elsewhere. The answer would undoubtedly be in accord with what I have just said above. The brachycera are the most highly specialized insects; the structural differences between the larva and imago are the most profound; their metamorphosis is the most complete; but two or three of the functional, larval organs remain functional during the metamorphosis; amoeboid blood corpuscles in the form

of phagocytes consume the rest, sparing, however, also the imaginal discs from which the imaginal organs are built up. Among the other holometabolic insects, on the other hand, many or most of the larval organs remain functional during the metamorphosis, hence there is but little histolysis. But the larval intestine would always necessarily become unfunctional, and, as we have seen, Kowalevsky is of the opinion that the larval midgut in all holometabolic insects contains imaginal discs and undergoes degeneration during the metamorphosis.

It is interesting to note that each of the three thoracic and eight abdominal segments which make up the larval body in the brachyceran dipters has two pairs of imaginal discs, a dorsal and a ventral pair. Thus there is a double row of discs extending the length of the body on the dorsal side and another on the ventral side of the larva. This is seen especially well in *Melophagus* where the thoracic discs are near the surface and not in the center of the larva as they are in *Musca*; the thoracic discs are here in straight rows with the abdominal ones. The question now presents itself,—are the thoracic and abdominal discs homodynamous organs. The different discs furnish very different imaginal organs: legs, wings, pupal spiracles, balancers, and hypodermis grow from the thoracic, and hypodermis, rectal glands, and perhaps external sexual organs from the abdominal discs; but yet they are all similar to each other in several very important respects. In the first place the method of ori-

gin is exactly the same in all. They all arise as ectodermal thickenings either in the embryo or in the larva; and further, the position of each pair whether dorsal or ventral, in each segment whether thoracic or abdominal, is the same as that of every other pair. The thoracic thickenings, it is true, develop further and become folds or pockets of the ectoderm because they must furnish the legs and wings of the imago, while the abdominal discs do not develop into pockets, with the exception of those of the external sexual organs*. Then again the thoracic and abdominal discs are alike in that they all help to form the imaginal hypodermis.

It seems to me that the *ventral* thoracic and abdominal discs at least, are homodynamous organs. There can be no doubt that the ventral discs of the different thoracic segments are homodynamous among themselves, likewise the ventral discs of the different abdominal segments among themselves. The ventral thoracic discs, too, are undoubtedly homologous to the thoracic extremities of the other insects; and I think there can be no doubt that the ventral abdominal discs are homologous to the rudimentary extremities which appear in the embryos of all other insects, *but not in the brachyceran dipters*. But the thoracic and the embryonic abdominal extremities in other insects are undoubtedly homodynamous organs, therefore, the ventral thoracic and abdominal imaginal discs in the brachycera

are also homodynamous organs, as things which are equal to the same thing are equal to each other. In the thorax these organs furnish the legs and the ventral half of the imaginal hypodermis, in the abdomen they furnish only the hypodermis, there being no legs. The two pairs of discs which furnish the external sexual organs are, I think, the ventral discs of the absent ninth and tenth abdominal segments.

When we consider the dorsal discs we find the matter is much more difficult. We cannot prove that the dorsal thoracic and the dorsal abdominal discs are homodynamous in the same way, because the dorsal abdominal surface of the insect has no extremities and no rudiments of any at any time. But I think, although reasoning from analogy is very unsafe in such matters, it is at least very probable that the same homodynamy exists on the dorsal side as on the ventral side of the insect. The dorsal discs have exactly the same appearance on the thorax and abdomen as the ventral discs, and the same method of origin, and if these facts go for anything there can be no doubt of the homodynamy.

If, now, this is really the case, what is its significance? The ventral discs, thoracic and abdominal, are homologous to extremities. The dorsal thoracic discs are homologous to wings. If they and the dorsal abdominal discs are homodynamous organs, are the latter homologous to wings, too? Such an assumption is of course impossible, but it is not impossible that there

* Pratt. l. c. p. 107.

existed in some previous phyletic stage, paired rows of external, segmental organs running down the back of the insect from one end to the other, just as the legs at one phyletic period extended the entire length of the ventral surface, and still do in the very lowest insects, and further, that on the thorax these organs developed finally, in the evolution of insects, into wings. Tracheal gills might represent such organs. And the fact that the dorsal prothoracic discs in *Musca* and the nematocera develop into the pupal spiracles lends great weight to this notion as these, like the tracheal gills, are respiratory organs. The well known theory of Gegenbaur and Lubbock, tracing the origin of wings in insects to tracheal gills, seems thus to obtain a new support.

Another matter which seems worth mentioning is that in different holometabolic insects, the extremities or the thoracic and abdominal imaginal discs (when such are present) may appear at very different times in the ontogeny. In some insects these appear early, and in some late, in the embryonic development, in some early, and in some

late, in the larval development. For instance, in the lower orders of holometabolic insects, as in those having incomplete metamorphosis, the anlagen of the extremities appear very early in the embryo. In *Melophagus* the thoracic discs, homologous organs, appear rather late in the embryo, while the abdominal discs appear probably early in the larval period. In *Corethra* the imaginal discs, also homologous to extremities, delay their appearance until just before pupation. Thus the epigenetic period in insects, when new organs are forming, does not end with the birth of the larva from the egg, but extends over the larval and even over the pupal period. The embryonic development of the insect really does not end until the imago bursts from the puparium, the embryonic, larval, and pupal periods being essentially identical. The principal significance of the pupal period and the metamorphosis is that it is the time when the larval characters which were adopted for use during a period of free life in the midst of the development, and which would be valueless to the imago, are corrected or abandoned.

DIAPHEROMERA FEMORATA.

I FIND among my notes the following observations on this insect in captivity.

The general color of the female is brown, marked by streaks and dots of a lighter brown or shaded darker at the sides of the body and at each joint. The face is orange, the antennae and palpi brown. The legs have a greyish green tinge and are lighter

than the body, but darker at the ends of the joints. The fore legs are always different in color from the others being brown above and dull yellow below and when stretched forward beside the appressed antennae (which just surpass them), as is always the case at rest, they make the insect appear a third longer than it is. They eat the edge of a leaf, usually straddling it with their legs and in an hour will devour a piece an inch long